



Hawkins, S., Bohn, K., Sims, D., Ribero, P., Faria, J., Presa, P., Pita, A., Martins, G., Neto, A., Burrows, M., & Genner, M. J. (2016). Fisheries stocks from an ecological perspective: Disentangling ecological connectivity from genetic interchange. *Fisheries Research*, 179, 333-341. <https://doi.org/10.1016/j.fishres.2016.01.015>

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This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Elsevier at <http://dx.doi.org/10.1016/j.fishres.2016.01.015>.

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Fisheries stocks from an ecological perspective: Disentangling ecological connectivity from genetic interchange

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Abstract

The concept of a stock of fish as a management unit has been around for well over a hundred years, and this has formed the basis for the fisheries science. Methods for delimiting stocks have advanced considerably over recent years, using including genetic, tagging and phenotypic information. In parallel with these developments, concepts in population ecology such as meta-population dynamics and connectivity have advanced. The pragmatic view of stocks has always accepted some mixing during spawning, feeding and or larval drift. Here we consider the mismatch between ecological connectivity of a matrix of populations typically focussed on demographic measurements, and genetic connectivity of populations that focus on genetic exchange detected using modern molecular approaches. We suggest that from an ecological-connectivity perspective populations can delimited as management units if there limited exchange during recruitment or via migration in most years. However from a genetic-connectivity perspective such limited exchange can maintain panmixia. We use case-studies of species endangered by overexploitation and/or habitat degradation to show how current methods of stock delimitation can help in managing populations and in conservation.

Keywords: Marine stock assessment, metapopulation, telemetry, molecular markers, ecological connectivity

Introduction

The concept of a ‘stock’ as a population unit that forms the basis of assessment and management is deeply rooted in fisheries science and practice. Russell (1931) was a pioneer in formalizing how a stock of fish would change over time due to recruitment, growth, fishing and natural mortality:

$$S_2 = S_1 + (R + G) - (F + M)$$

where S_2 is stock in year 2, S_1 is stock in Year 1, R = recruitment to the fished stock, G is growth of individuals in the fished stock, F is fishing mortality and M is natural mortality.

This straightforward expression helped to form the basis of contemporary quantitative fisheries science. This includes informing the Beverton-Holt yield per recruit equation, formulated manage growth overfishing typical of long-lived demersal fish species, such as flatfish and gadoids (Beverton and Holt, 1957). Russell’s equation first defined the terms used to understand the relationship between recruitment and stock (Shepherd, 1982), but it had no terms for emigration or immigration and assumed these to be negligible or balanced in exchange with other populations. Advances in theory and empirical observations have shown that this assumption is rarely true, so an understanding of the degree of interchange between populations is crucial to managing exploited species.

A key assumption of fisheries management is that a stock or management unit can be rigorously defined. However, the formal definition of “stock” has remained a challenge for over 100 years of fisheries science (Begg et al., 1999, Booke, 1999, Cadrin et al., 2013). In this review we discuss how this traditional concept in fisheries biology has been informed by recent advances in molecular genetics and population ecology, especially the emerging theory of metapopulation dynamics. We first return to basics and consider fish life histories, and consider where mixing occurs between stocks. We then introduce tools that can used to quantify the segregation of stocks at different stages of their life history. We then provide a brief introduction to metapopulation dynamics and consider examples of where it has been applied to exploited finfish and shellfish species. Next, we use a series of case studies to illustrate how telemetric, ecological and molecular genetic approaches provide

insights into stock definition. A recurring theme in this review are the differences between genetic interchange of populations, and the extent of interchange of individuals among ecologically-connected populations.

Basic life history concepts and traditional tools

A useful starting point for consideration of the stock concept in fully marine systems is to consider life history patterns. In finfish that can undergo extensive circuits of migration, the classic Harden-Jones triangular model (Harden-Jones, 1968) is a helpful simplification of a typical life history (Fig 1a). Under this model regional scale (100-1000 km) current patterns provide the environmental context for life histories of teleost fish with pelagic larval stages. These fish aggregate to spawn, and engage in broadcast spawning and external fertilisation. Aggregation usually occurs by swimming against currents. However Metcalfe et al. (2002) provide an example of tidal stream transport to spawning grounds. Post-spawning eggs and larvae drift with the currents until they end up on juvenile nursery grounds, while spent adults drift back to adult feeding grounds. After a period of time in nursery grounds which are often shallow, highly productive and provide some refuge from predators, juveniles migrate against currents to adult feeding grounds. From there, the cycle resumes by counter-current migration to spawning grounds. For a particular species of fish there may be several distinct stocks, sometimes overlapping temporally and geographically during cycles of migration. Some of the earliest work in contemporary fisheries sciences focussed on defining such stocks, for example Atlantic herring (*Clupea harengus*) on the European shelf in the late 19th and early 20th century (Cushing, 1967).

The Harden-Jones Model can be easily extended to migratory fish that spawn in freshwater (salmonids, alosines, lampreys) or the sea (anguillid eels). It is not applicable to sessile or highly sedentary shellfish, and here source-sink metapopulation models are more applicable. Many shellfish do, however, have distinct settlement sites or nursery areas (e.g. scallops, mussels, limpets) but the distance moved from the adult site is often very small (1–10m). In these cases nurseries for sedentary

species are mosaics of suitable habitat scattered among adults, for example rock pools in the case of intertidal limpets (Lewis and Bowman, 1975) or algal turfs in the case of primary settlement of intertidal mussels. Sometimes adult shells provide the nursery for juveniles, as is the case for some limpets (Branch, 1975).

There is extensive “traditional” evidence discrete subpopulations (or stocks) of many marine fishes, based on morphological characters, spawning phenology and tagging data. Examples include Atlantic herring (Smith and Jamieson, 1986), European plaice (*Pleuronectes platessa*) (Hunter *et al.*, 2004) and Atlantic cod (*Gadus morhua*) (Smedbol and Wroblewski, 2002). There is however little evidence of strong population genetic structure over regional spatial scales in any of these species. This could, in some cases, result from drift in the plankton and on shared inshore nursery grounds, before populations segregate on the basis of non-genetic cues. Alternatively, adult movement could lead to extensive mixing of stocks occurs during the adult phase on spawning grounds (Hunter *et al.* 2004), where exchange of genetic material presumably occurs and prevents evolution of genetic differentiation. Such adult migrations could be over long distances (> 1000 km), such as the migration that leads to broad-scale genetic similarity among stocks of European hake (*Merluccius merluccius*) (Pita *et al.*, 2011).

The approaches used to define stocks are varied (Fig 1b). These range from conventional tags with individual identifiers (e.g. Kleiber *et al.*, 1987, Begg and Waldman, 1999; Kohler and Turner, 2001), to meristic counts of fin rays or vertebrae (e.g. Meng and Stocker, 1984). Parasites have long been recognized as potential biological tags (Lester, 1990), while more recently telemetry based on electronic tags has been used to define movements of larger fish such as basking sharks (Sims, 2010). Advances in technology are driving the miniaturisation of devices, enhancing memory capacity and enhancing the spatial scale of studies through satellite linkages (Priede, 1984, Sims *et al.*, 2009, Sims, 2010). Now, a wide range of fish species have now been tagged, for including Atlantic cod, European hake and anglerfish (*Lophius piscatorius*) (de Pontual *et al.*, 2013, Righton *et al.*, 2006, Turner *et al.*, 2002, Wearmouth *et al.*, 2014). However, these fish are mainly large-bodied and/or in the adult phase,

although tagging of wild juvenile fish for telemetry is technically feasible (McMichael et al., 2010). Additionally methods such as passive integrated transponder (PIT) tagging with unique individual 'bar codes' allows juveniles to be tagged because the tags are small and no bulky batteries are required (Gibbons and Andrews, 2004, Skalski et al., 1998). However, long-term, long-range telemetric tracking for most species is limited by the challenge of fish size on the nursery grounds. Thus using traditional or telemetric methods, typically only the adult, subadult and late juvenile phases of migration are tractable to study (Sims, 2010). As an alternative to traditional methods of stock delimitation, in the 1970s, genetic-based methods we tested and have since increased in prevalence. Early work used allozymes (Grant et al., 1980, Mork et al., 1985), whereas subsequently, assays of mitochondrial and nuclear DNA sequence variation have been more commonly used. In parallel there have been significant developments in the application of geochemical analytical methods to quantify sclerochronological records in otoliths, scales and shells (Fig 1c).

The Metapopulation Concept and Connectivity

The metapopulation concept provides a valuable theoretical framework for discussing the spatial and temporal dynamics of fish stocks. Going back to the early ideas of island biogeography proposed by MacArthur and Wilson (1967) and first formulated by Levins (1969), a metapopulation is today defined as any 'assemblage of discrete local populations with migration between them' (Hanski and Gilpin, 1997). Extinctions of local populations may occur. However, their subsequent recolonization through the dispersal by a few individuals will result in the long-term persistence of this 'population of (sub-) populations'. The level of connectivity between the local populations as well as differences in features of the local habitats lead to a range of possible metapopulation systems (Harrison and Taylor, 1997, Fullerton et al., 2011, Fig. 2). The classical metapopulation consists of similar, discrete populations (Fronhofer et al., 2012). These are connected by relatively rare dispersal events that only just prevent complete isolation of the individual populations (Fig. 2b). If, however, connectivity is very low, this may lead to a non-equilibrium metapopulation consisting of completely isolated local populations (Fig 2c). Here, persistence of the individual populations is unlikely as recolonization from

neighbouring populations following local extinction events is unlikely. On the other end of the ‘dispersal scale’, complete mixing of these populations would likely result in a single large panmictic population (Fig 2a). In the case of non-equilibrium, classical and panmictic metapopulations habitat quality and local population sizes are relatively equal. However mainland-island metapopulations are characterised by sharply contrasting population sizes (Fig 2e). Particularly large populations contribute most to connectivity of the metapopulation system and, by re-colonising smaller populations that would not be able to persist without such input, this results in the persistence of the metapopulation. Source-sink metapopulations are similarly characterised by ‘donor’ and ‘receptor’ populations. Here the ‘sink’ feature stems from poor habitat quality rather than from small population size (Harrison and Taylor, 1997, Fronhofer et al., 2012).

Many anadromous fish species such as the sockeye salmon (*Oncorhynchus nerka*) display characteristics of metapopulation systems (Quinn et al., 2012, Peterson et al., 2014). Schtickzelle and Quinn (2007) list three conditions that are essential for the metapopulation concept to apply, and, after reviewing the life history traits of the sockeye salmon, found these to be fulfilled. First, the habitat patches inhabited by the local populations have to be discretely disconnected by a ‘matrix’ of unsuitable habitats. This is the case for sockeye salmon, as limited movement of the males during the spawning season takes place within but not between sites, resulting in distinct populations. Second, the dynamics of the local populations must be somewhat asynchronous, decreasing the likelihood of extinctions of the whole metapopulation complex through simultaneous local extinctions. This, too, is likely the case for *O. nerka* as several studies have found that correlation in survival rates between populations is low (Peterman et al., 1998, Stewart et al., 2003), allowing for recolonization events from neighbouring populations to take place in case of local extinctions. Third, some dispersal between the local populations must occur, as in sockeye salmon when single individuals stray to other populations during spawning (Schtickzelle and Quinn, 2007).

The metapopulation concept provides a framework in which to define suitable management units. For species with source – sink characteristics, such as many shellfish species, it places the emphasis on

management of the source population. At the other extreme, metapopulations approaching panmixia need to be considered as an integrated single unit. In the case of occasional exchange between populations then the management unit or stock would be at the subpopulation level. In the next sections we provide examples of where each of the approaches outlined above has been used to investigate spatial dynamics, population ranges and the stock concept in fisheries.

The concept of metapopulations in open ecosystems requires estimates of connectivity, which can occur in different ways, and over different spatial and temporal scales. Ecological connectivity can be broadly thought of as the movement of individuals and associated resources among habitat patches. For example, in aquatic systems energy and carbon is exchanged between habitats through detritus and movement of individuals. A notable case is migration of salmonids from offshore marine feeding grounds to inland rivers, where the carcasses of spent fish contribute essential nutrients to both the riverine and terrestrial riparian habitat (Cederholm et al., 1999). Such ecological connectivity can occur at a variety of spatial scales, and usually is less than 10s of kilometres, but can occasionally be substantial such as in the case of long-distance rafting of seaweeds (Ingólfsson, 1995).

Nested within the broader concept of ecological connectivity is that of demographic connectivity, which occurs between population units either by interchange of migrating adults, subadults or juveniles, or exchange of planktonic larvae. In many marine species connectivity occurs primarily at the larval stage, and often with net exchange in one direction from a source to sink populations. Thus, in marine systems demographic connectivity is commonly determined by propagule pressure and the permeability of environment between favourable habitat patches, which is often determined by direction of currents. For a set of populations to be demographically connected, significant exchange should occur in the majority of years if the net direction and volume of exchange differs.

Population genetic methods typically estimate a measure of genetic connectivity by the extent of allele sharing at the population level. It is much less common for genetic approaches to be used to identify individual migrants, although it is possible (e.g. Simpson et al. 2014). Depending on adult

population size, exchange of individuals between populations only needs to occur infrequently to maintain panmixia. Genetic connectivity can be considered from the perspective of its effects on adaptation and inbreeding (Lowe and Allendorf, 2010). Low levels of genetic connectivity can be considered as “adaptive connectivity”. Here low gene flow is sufficient to spread advantageous alleles, and the resultant high levels of genetic differentiation can promote fixation of these alleles by selection. Moderate levels of genetic connectivity can be considered as “inbreeding connectivity”. Here moderate gene flow will be sufficient to avoid problems with inbreeding, but differences in allele frequencies and the effects of selection will be harder to detect. High levels of genetic connectivity can be considered as “drift connectivity”. Here the substantial gene flow maintains similar allele frequencies, and we may expect evolutionary divergence will occur primarily through drift rather than selection (Lowe and Allendorf, 2010). Fundamentally, therefore, the concepts of ecological-demographic connectivity and genetic connectivity are very different. Demographic connectivity focusses on quantifying the flow of individuals irrespective of reproductive contributions to the population, while genetic connectivity focusses on the number of migrants that ultimately reproduce and share alleles between populations.

Case study 1: Management insights from telemetric studies

Recently, telemetry (or biologging) tagging studies have demonstrated that relatively inexpensive tags can be used to determine of spatial movements and behaviour patterns of hundreds of individuals from a single species over multiple annual cycles (Block et al., 2005, Block et al., 2011, Humphries et al., 2010, Righton et al., 2010). Telemetry is fast transforming into a means to understand spatial dynamics and migrations at the population level. In the future this technology is likely to take an increasing role in the management of population units as it becomes cheaper and miniaturises further. However, despite the recent progress, there are relatively few clear examples of cases in which electronic tracking of a relatively few individuals has resulted in species management action. Basking sharks (*Cetorhinus maximus*) provide at least one example of the power of telemetric tracking of migratory movements of adults for conservation action.

239

240 The iconic basking shark is the world's second largest fish species, reaching up to 12 m in length and
241 approximately four tons in weight (Sims, 2008). Organised fisheries for basking shark have existed in
242 the north-east Atlantic region since at least 200 years ago (Fairfax, 1998), and the earliest directed
243 fisheries for pelagic sharks were probably for this species (Pawsons and Vince, 1999). The basking
244 shark is at particularly high risk from overexploitation, even among elasmobranchs. This because in
245 addition to slow growth and late sexual maturity, their fecundity is among the lowest for any marine
246 vertebrate species with approximately six offspring per mature female produced every second or third
247 year (Sims, 2008). By the 1990s there was concern within the UK government, the national statutory
248 agencies and among conservation groups that populations of basking sharks were in low numbers.
249 Although reliable population size estimates were lacking, declines in directed fishery catches had
250 been documented since the 1950s. As an indicator of the extent of historic fishing, records suggest
251 that between 1946 and 1997 in the north-east Atlantic an estimated 105,730 mature basking sharks
252 were killed, landed and processed for meat and oil (Sims and Reid, 2002).

253

254 Basking sharks were protected in UK territorial waters in April 1998, largely as a result of applying
255 the precautionary principle. There was a need to understand spatial movements to make progress in
256 broadening conservation, and this was mainly because previous proposals to list basking sharks under
257 the Convention for International Trade in Endangered Species (CITES) Appendix II had failed. This
258 failure was in part because it was unclear whether basking shark regional declines were genuine, and
259 not a result of large-scale shifts in distribution. In 2001-2002, however, basking sharks tagged off the
260 UK were tracked for up to nine months using newly available satellite-linked archival transmitters
261 (Sims et al., 2003, Sims et al., 2005). Tracking showed that although *C. maximus* moved long
262 distances over several months (up to 3,400 km in 5 months) and across European national boundaries,
263 they largely remained faithful to productive front habitats of the north European continental shelf and
264 shelf-edge habitats (Sims et al., 2003). This suggested that a basking shark 'stock' was centred on the
265 North-East Atlantic year-round. Therefore, catch declines observed over the previous decades were
266 less likely due to emigration, and instead were more likely to be reflective of real declines in

population abundance across the region (Sims et al., 2005). The tracking data were incorporated into the UK-led proposal that gained successful listing for basking sharks on CITES Appendix II in 2002 that was enforced from February 2003. This was a watershed for CITES because not only was it the first shark to be listed, but it was also the first commercially exploited marine fish.

Since 2003 the basking shark has been the subject of growing protection as a potentially endangered species (Sims, 2008). A study by Southall et al. (2006) demonstrated the extent of seasonal migrations of basking shark in the various waters around the U.K., Ireland and France, and into international waters. In particular, sharks from the English Channel were shown to migrate from the Channel through the Irish Sea or around Ireland up into Scottish waters. These extensive migrations also placed basking sharks at risk in international waters and demonstrated the need to view the management unit as one of the whole North East Atlantic out to the shelf edge. In November 2005 this information led to basking sharks being afforded protection under Appendix II of the Convention for the Conservation of Migratory Species of Wild Animals (CMS) (Sims, 2008). Furthermore, the listing of basking shark by CITES and CMS led to an outright ban on European Community vessels catching, keeping on board, or landing basking sharks inside and outside European waters from 2007 onwards (Article 5.6, EC regulation no. 41/2007), thus making the basking shark one of the most protected species of shark (Sims, 2008).

Case study 2: Ecological connectivity in rocky shore assemblages

Extensive long-term datasets exist for many rocky shore assemblages (Mieszkowska et al., 2014). Where such datasets are spatially explicit they provide the opportunity to examine temporal concordance of recruitment within species. In principle, a high degree of synchrony among populations may be considered indicative of extensive spatial mixing of larvae among populations. Alternatively, synchronised fluctuations in larval supply driving later synchrony of breeding in sessile or sedentary adult populations (e.g. in barnacles, Kendall et al., 1982). Finally, such synchronisation among otherwise isolated populations could be driven by an extrinsic environmental factor operating

at a large spatial scale, as has been shown among Soay sheep populations on islands in the St. Kilda archipelago (Grenfell et al., 1998).

This general approach of studying intraspecific recruitment synchrony has been used to form the basis of comparisons among species with different life history traits. Using long-term monitoring data from around the Sullom Voe oil terminal in Shetland, Burrows et al. (2002) quantified the degree of recruitment synchrony of several rocky shore species. The barnacle *Semibalanus balanoides* with at least four weeks in the plankton showed the most spatial synchrony in recruitment. This was much less in species with shorter-lived planktonic larvae such as the limpet *Patella vulgata* and the non-planktonic direct developers such as *Littorina saxatilis*, *Littorina obtusata* and *Nucella lapillus*. This research showed that there was concordance and hence high ecological connectivity over scales of 10s of kilometres on a complex coastline for species with long-lived planktonic larvae. In contrast, the population dynamics of other species is very typical of the small-scale patchiness typical of many rocky shore assemblages driven by a combination of external stochastic factors and complex internal interactions (Hartnoll and Hawkins, 1985, Burrows and Hawkins, 1998, Johnson et al., 1997, Johnson et al., 1998).

Case study 3: Molecular genetic data and fish conservation

In recent years molecular genetic data have been used to inform the management of endangered fish species. Here we give examples from species of skate, sea lamprey and shad to illustrate how these data can address broad aspects of species life histories relevant to spatial management.

Dipturus batis was sufficiently abundant enough in coastal waters of the U.K. in the late 19th century to be called the “Common Skate” (Heape, 1888, Clark, 1922). But following decades of exploitation by trawling and bottom-set long-lining it had become biologically extinct across much of inshore waters around the British isles by the 1970s (Brander, 1981). Recent work using mitochondrial and nuclear microsatellite markers examined the spatial genetic structure of common skate in shelf seas

around the U.K. and Ireland using samples from survey cruises, anglers and bycatch. This work threw up a major surprise. Two genetically distinct and geographically disjunct clades of “common skate” were identified, and when placed into the context of other European skates they were shown not to be sister clades (Griffiths et al., 2010). These two clades have clearly defined temperature optima with a “northern” clade being bounded by warmer summer water conditions greater than 17 °C, whilst a “southern” clade is bounded by cold winter temperatures of <8 °C. In this case, genetic studies alongside morphological evidence from a parallel study (Iglésias et al. 2010), have helped define the target taxa for conservation action. They have clearly demonstrated a species that has been listed by the International Union for Conservation of Nature as Critically Endangered is actually two taxa, each with a much smaller geographic range. These data provide clear grounds for each taxon to be further listed as Critically Endangered species. Clearly management and conservation initiatives need to be revisited in light of these results (Neat et al., 2014).

Sea lamprey (*Petromyzon marinus*) is a migratory species that are typically marine and parasitic as adults, migrate to spawn in freshwater, and are freshwater sediment feeders as juveniles. Genetic work revealed a pan-Atlantic species with two clearly defined stocks on each side of the Atlantic (Genner et al., 2012). The weak genetic structure on each continental seaboard is consistent with a lack of natal homing and a lifestyle involving extensive journeys as an ectoparasite on large hosts that undergo extensive migrations including minke whales (Nichols and Tscherter, 2011) and basking sharks (Wilkie et al., 2004). From a conservation perspective, an integrated North American or European view has to be taken as each is a panmictic stock needing protection in all the rivers in which successful spawning and nursery areas occur.

A more complex picture has emerged with two closely related and endangered species of alosines in European waters, the allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*). These large migratory clupeids typically occupy marine environments as adults, but enter rivers to spawn. These species overlap in their breeding grounds, and reproductive barriers between these two species are breaking down. Hybridization, which was evident from morphology, has been confirmed using genetic

methods (Jolly et al., 2011). Up to 70% of individuals within a breeding population can have some hybrid origin (Jolly et al., 2012). Insight of the genetic structure of the pure species has been gained using microsatellite markers. The land-locked subspecies of the twaite shad found in Lough Leane, Ireland, (*A. fallax killarnensis*) was shown to be highly genetically distinct from fully migratory populations in British and Irish waters. In the twaite shad there was isolation by distance suggesting limited gene flow between breeding populations and consistent with natal homing (Jolly et al., 2012). In the allis shad, two genetic clusters of breeding individuals were revealed, one in the Solway Firth in the northern Irish Sea, and second associated with the Tamar river South-West of England. These distinct populations clearly require targeted local action plans to help conserve and preserve their limited breeding populations.

Case study 4: Shellfish stocks – Exploitation and connectivity of limpet populations

We draw on genetic work on limpet populations in archipelagos and on linear coastlines. Limpets are heavily exploited in several regions of the world, for example South Africa, Chile and Hawaii (Castilla and Duran, 1985, Siegfried et al., 1994, Branch and Odendaal, 2003). In the Macaronesian Islands (Azores, Canaries, Madeira) and Mediterranean several species of *Patella* are at risk from overexploitation (Templado, 1997, Hawkins et al., 2000). In the Azores, stocks have been under pressure since the 1980s with the endemic species, *Patella aspera* and *Patella candei*, being at risk (Hawkins et al., 2000, Martins et al., 2008). Genetic work using allozymes (Côrte-Real et al., 1996a, Côrte-Real et al., 1996b, Weber and Hawkins, 2002, Weber and Hawkins, 2005) and mitochondrial DNA markers (Koufopanou et al., 1999, Sa-Pinto et al., 2008) has confirmed the endemic nature of the species on the islands compared to the mainland. The mainland *Patella ulyssiponensis* is a direct sister taxon to *P. aspera* endemic to the Macaronesian Islands. *P. candei* is a complex of species with clades associated with each island group.

More recent work has used microsatellite markers to understand connectivity across and within archipelagos in Macaronesia to define stocks of exploited species (Faria et al., 2015). Using a suite of

polymorphic markers derived from next generation sequencing, *P. aspera* was shown to have one unstructured population in the Azores, which was significantly different to the population on the Canaries. This was despite the highly scattered nature of the Azorean archipelago with widely separated Western, Central and Eastern group of islands. Thus, *P. aspera* on the Azores is a classic metapopulation, with spatially separated populations connected by larval exchange. Furthermore, the detection of significant inbreeding (F_{IS}) estimates using the Chybicki and Burczyk (2009) approach suggests a relatively small effective population size, perhaps due to the lack of large females as a result of exploitation of this protandric species. These results indicate that if statutory conservation measures such as closed seasons, minimum catch sizes, licensing of commercial limpet collectors and Marine Protected Areas are enforced (Martins et al., 2011), then recovery of the very sparse populations in the Eastern Group (Sao Miguel and Santa Maria islands) should be possible from the healthier, less-exploited populations in the Central and Eastern Groups (Martins et al., 2008). These results suggest that limpet conservation and fisheries management in the Azores needs to be viewed from a whole archipelago perspective. Very limited genetic and individual exchange with the Madeira and Canaries archipelagos would inhibit the re-population of depleted Azorean stocks. Notably, limpets in these other archipelagos are also under pressure (Côte-Real et al., 1996a, Ferraz et al., 2001, Navarro et al., 2005, Nunez et al., 2008).

Population genetics has been used to assess connectivity in the largely unexploited *Patella rustica* which has shown recent shifts in range extent on the Iberian coastline in response to climate change (Lima et al., 2006, Lima et al., 2007). This is a typically warm-temperate species which occurs on the Atlantic coast of North Africa and throughout the Mediterranean. However it has historically had a large distribution gap, being absent from Central Portugal to Galicia, before re-appearing on the Asturian and Basque coasts, and continuing to a northern limit on the last rocky substrate of the Basque coastline around Biarritz (Nobre, 1940, Fischer-Piette, 1963). Regional warming appears to have led to the recent colonization of this historical gap from the late 1990s and early 2000s, and it does not appear to be an ephemeral event. Densities at newly-colonised sites have been steadily increasing since the biogeographic gap since 1990s, although remaining considerably below the

values recorded within historical range in southern Portugal (Sousa et al., 2012). The colonisation event demonstrates that larval dispersal from neighbouring populations does occur to some extent, but not necessarily in large numbers. Despite the long-standing nature of the distributional gap, Ribeiro et al. (2010) found no evidence of genetic differentiation between historical populations on either side of the former gap using microsatellite and mtDNA markers. This suggests that the Iberian-Atlantic coast is inhabited by a single metapopulation, and that the gap was not an effective barrier to gene flow or it did not last long enough (at least 70 years) for genetic differentiation to occur. In species typically possessing high effective population sizes, as is the case of patellid limpets, genetic drift can be very slow, and even very low levels of gene flow can be sufficient to homogenize gene frequencies (Slatkin, 1993). In this case, occasional larval exchange across the stretch of inhospitable habitat in north-western Iberia may have been sufficient for genetic panmixia; but clearly there had been little significant ecological connectivity for many decades.

Moving forward

Genetic approaches can give insights into gross definition and extent of genomic admixture among management units which may be important in conserving biodiversity especially of slowly overexploited species at risk of extinction. Recent molecular techniques are increasing our ability to look at genome-wide polymorphism, not only improving our understanding of population demography and structure, but also uncovering adaptive genetic differentiation in species which are genetically homogeneous at neutral loci over broad spatial scales (e.g. Bourret et al., 2013, Hess et al., 2013, Wit and Palumbi, 2013). Population genomics can thus provide vital information for fisheries management and species conservation, as it can potentially revolutionize the delineation of conservation units, as well as our understanding of the adaptive response of populations to rapid environmental change and the evolutionary consequences of selective harvesting (Nielsen et al., 2009, Funk et al., 2012). Nevertheless, genetic approaches will not be able to quantify the true levels of demographic connectivity and the ecological effects of movement. Population genetic estimates of

genetic connectivity are rarely coupled with methods for measuring demographic connectivity, and thus there is currently little understanding the relationship between the two variables.

The way forward is to apply a battery of techniques being fully aware of the advantages and limitations of each. Geochemistry may provide some insights into the parts of the life history that are less tractable to follow with tracking methods, such as movement in plankton and on nursery grounds (Carvalho and Hauser, 1995, Thorrold et al., 2002, Tanner et al., 2014). Computer simulations of particle dispersion patterns using real-temporal hydrographic data from eddies and local currents can also provide additional insights into larval dispersal and routes to nursery grounds (e.g. Schunter et al., 2011). Continuous tagging of hundreds of individual fish within a population using archival datalogging tags and/or satellite relay transmitters, may help us to better understand where adults and subadults movement behaviour, and consequently, how they can be better managed using spatial measures including adaptive closed areas, static marine conservation zones and specific fishing restrictions. Similarly, implantable PIT tags have the potential for monitoring post-larval and juvenile stages, but only if networks of PIT detectors are deployed and maintained widely in nursery areas to identify and log the presence (absence) of individuals. Population-level tracking of fish for sustainable fisheries management is becoming tractable and is one of the new frontiers in animal biologging science. Applying a range of techniques can give insights into the level of exchange of individuals between populations, hence its importance of migration. Only if there is considerable exchange would this prompt aggregating fish from different locations into management units.

Conclusions

Genetic methods provide a valuable toolbox for assessing dispersal paths and source-sink dynamics. Genetic estimates of connectivity, however, do not equate to ecological connectivity in the sense that genetic panmixia can result from occasional exchange per generation while for true ecological connectivity there needs to be significant exchange in most years. This mirrors the fisheries ecology perspective, where exchange between connected meta-populations should occur in most years for a

set of populations to be a realistic management unit. Population connectivity can be indicated by spatial concordance of recruitment, but this may be an intractable approach in a spatially extensive network of populations that needs to be monitored with high temporal resolution for a long-time (>10 years as in the rocky shore examples above, Burrows et al., 2002). Alternatively, there has to be suitable skeletal markers of age and hence age structure in long-lived populations. In heavily exploited populations, such longevity is rare. Finally, it is worth considering that even if greater genetic resolution was possible, there will be a temporal disconnect between the evolutionary processes that drive genetic differentiation over generational timescales (Waples, 1998), and the ecological-demographic connectivity that takes place over interannual timescales. Nevertheless, the methods that can be used to measure these differences in connectivity are all potentially informative as long as the difference between genetic and ecological-demographic connectivity is understood. This needs to be alongside a good comprehension of other fundamental aspects of species biology, including life-history traits, habitat utilisation and extrinsic influences on demography.

Acknowledgements

Work in this paper was funded by the U.K. National Environmental Research Council (NERC) grant-in-aid to the Marine Biological Association of the U.K., and the Ocean 2025 Strategic Research Programme to SJH, DWS and MJG. The Esmée-Fairbairn foundation supported work on endangered fish species. Fundação para a Ciência e a Tecnologia Portugal funded work on limpets in the Azores and mainland Portugal. PR was supported by FCT grants SFRH/BPD/69232/2010 and PTDC/MAR/121016/2010 funded through QREN and COMPETE. GMM was supported by FCT grant SFRH/BDP/63040/2009.

Figure Legends:

Fig. 1a) The Harden-Jones (1968) model illustrates patterns of fish migration between spawning grounds, nursery grounds and feeding grounds. b) Various traditional and more contemporary

techniques (upper case italics) have been used for direct tracking of individuals and for definition of stocks. c) More modern indirect methods (upper case italics) such as genetics, geochemistry and larval dispersal modelling. Solid arrows indicate main pathways of migrations and dashed arrows secondary pathways of migrations. Curved arrows indicate dominant direction of currents.

Fig. 2) Variation in the structure of metapopulations depending on the degree of connectivity (y-axis) and the number of individuals involved (x axis). Illustrated are: a) a panmictic metapopulation, b) a classic metapopulation, c) a non-equilibrium metapopulation, d) patchy populations, e) a mainland-island or source-sink metapopulation, and f) very low dispersal populations. Filled and empty patches represent existing and extinct populations, respectively. The direction of the arrows marks the direction of dispersal between populations. Dashed and solid arrows indicate past (extinct) and existing dispersal connections, respectively. Note panels d and f are not discussed in the text, as these scenarios are not considered metapopulations. The figure is adapted from Fullerton et al. (2011) and Harrison and Taylor (1997).

References

- Begg, G.A., Friedland, K.D., Pearce, J.B. (1999) Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research* **43**, 1-8.
- Begg, G.A., Waldman, J.R. (1999) An holistic approach to fish stock identification. *Fisheries Research* **43**, 35-44.
- Beverton, R.J.H., Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*, Chapman & Hall, London.
- Block, B.A., Jonsen, I., Jorgensen, S., et al. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86-90.
- Block, B.A., Teo, S.L., Walli, A., et al. (2005) Electronic tagging and population structure of Atlantic Bluefin Tuna. *Nature* **434**, 1121-1127.
- Booke, H.E. (1999) The stock concept revisited: perspectives on its history in fisheries. *Fisheries Research* **43**, 9-11.

519 Bourret, V., Kent, M.P., Primmer, C.R., *et al.* (2013) SNP-array reveals genome-wide
 520 patterns of geographical and potential adaptive divergence across the natural range of
 521 Atlantic salmon (*Salmo salar*). *Molecular Ecology* **22**, 532-551.
 522 Branch, G. (1975) Intraspecific competition in *Patella cochlear* Born. *Journal of Animal*
 523 *Ecology*, 263-281.
 524 Branch, G., Odendaal, F. (2003) The effects of marine protected areas on the population
 525 dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave
 526 action. *Biological Conservation* **114**, 255-269.
 527 Brander, K. (1981) Disappearance of common skate *Raia batis* from Irish Sea. *Nature*, **290**
 528 Burrows, M., Hawkins, S. (1998) Modelling patch dynamics on rocky shores using
 529 deterministic cellular automata. *Marine Ecology Progress Series* **167**, 13.
 530 Burrows, M.T., Moore, J.J., James, B. (2002) Spatial synchrony of population changes in
 531 rocky shore communities in Shetland. *Marine Ecology Progress Series* **240**, 39-48.
 532 Cadrin, S.X., Kerr, L.A., Mariani, S. (2013) *Stock identification methods: applications in*
 533 *fishery science*. Academic Press.
 534 Carvalho, G.R., Hauser, L. (1995) *Molecular genetics and the stock concept in fisheries*,
 535 Springer.
 536 Castilla, J., Duran, L. (1985) Human exclusion from the rocky intertidal zone of central
 537 Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos*, 391-399.
 538 Cederholm, C.J., Kunze, M.D., Murota, T., & Sibatani, A. (1999). Pacific salmon carcasses:
 539 essential contributions of nutrients and energy for aquatic and terrestrial
 540 ecosystems. *Fisheries*, **24**, 6-15.
 541 Chybicki, I.J., Burczyk, J. (2009) Simultaneous estimation of null alleles and inbreeding
 542 coefficients. *Journal of Heredity* **100**, 106-113.
 543 Clark, R.S. (1922) Rays and skates (Raiae). No. I: egg capsules and young. *Journal of the*
 544 *Marine Biological Association of the United Kingdom* **12**, 577-643.
 545 Côte-Real, H., Hawkins, S., Thorpe, J. (1996a) An interpretation of the taxonomic
 546 relationship between the limpets *Patella rustica* and *P. piperata*. *Journal of the Marine*
 547 *Biological Association of the United Kingdom* **76**, 717-732.
 548 Côte-Real, H., Hawkins, S., Thorpe, J. (1996b) Population differentiation and taxonomic
 549 status of the exploited limpet *Patella candei* in the Macaronesian islands (Azores,
 550 Madeira, Canaries). *Marine Biology* **125**, 141-152.
 551 Cushing, D. (1967) The grouping of herring populations. *Journal of the Marine Biological*
 552 *Association of the United Kingdom* **47**, 193-208.

- de Pontual, H., Jolivet, A., Garren, F., Bertignac, M. (2013) New insights on European hake biology and population dynamics from a sustained tagging effort in the Bay of Biscay. *ICES Journal of Marine Science: Journal du Conseil* **70**, 1416-1428.
- Fairfax, D. (1998) *The basking shark in Scotland: natural history, fishery and conservation*, Vol., Dundurn.
- Faria, J., Rivas, M., Martins, G., *et al.* (2015) A new multiplexed microsatellite tool for metapopulation studies in the overexploited endemic limpet *Patella aspera* (Röding, 1798). *Animal Genetics*, 96-97.
- Ferraz, R.R., Menezes, G.M., Santos, R.S. (2001) Limpet (*Patella* spp.)(Mollusca: Gastropoda) exploitation in the Azores, during the period 1993-1998. *Arquipklago. Life and Marine Sciences*. Supplement 2 (Part B): 59-65.
- Fischer-Piette, E. (1963) *La distribution des principaux organismes intercotidaux Nord-Iberiques en 1954-1955*, Masson.
- Fronhofer, E.A., Kubisch, A., Hilker, F.M., Hovestadt, T., Poethke, H.J. (2012) Why are metapopulations so rare? *Ecology* **93**, 1967-1978.
- Fullerton, A.H., Lindley, S.T., Pess, G.R., Feist, B.E., Steel, E.A., McElhany, P. (2011) Human Influence on the spatial structure of threatened Pacific Salmon metapopulations. *Conservation Biology* **25**, 932-944.
- Funk, W.C., McKay, J.K., Hohenlohe, P.A., Allendorf, F.W. (2012) Harnessing genomics for delineating conservation units. *Trends in Ecology & Evolution* **27**, 489-496.
- Genner, M.J., Hillman, R., McHugh, M., Hawkins, S.J., Lucas, M.C. (2012) Contrasting demographic histories of European and North American sea lamprey (*Petromyzon marinus*) populations inferred from mitochondrial DNA sequence variation. *Marine and Freshwater Research* **63**, 827-833.
- Gibbons, W.J., Andrews, K.M. (2004) PIT tagging: simple technology at its best. *Bioscience* **54**, 447-454.
- Grant, W., Milner, G., Krasnowski, P., Utter, F.M. (1980) Use of biochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 1236-1247.
- Grenfell, B., Wilson, K., Finkenstädt, B., *et al.* (1998) Noise and determinism in synchronized sheep dynamics. *Nature* **394**, 674-677.
- Griffiths, A.M., Sims, D.W., Cotterell, S.P., *et al.* (2010) Molecular markers reveal spatially segregated cryptic species in a critically endangered fish, the common skate (*Dipturus batis*). *Proceedings of the Royal Society B: Biological Sciences* **277**, 1497-1503.

587 Hanski, I., Gilpin, M.E. (1997) Metapopulation biology. Academic Press.

588 Harden-Jones, F.D. (1968) *Fish migration*. Edward Arnold Ltd., London.

589 Harrison, S., Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics.

590 *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego,

591 *California, USA*, 27-42.

592 Hartnoll, R.G., Hawkins, S.J. (1985) Patchiness and fluctuations on moderately exposed

593 rocky shores. *Ophelia* **24**, 53-63.

594 Hawkins, S., Corte-Real, H., Pannacciulli, F., Weber, L., Bishop, J. (2000) Thoughts on the

595 ecology and evolution of the intertidal biota of the Azores and other Atlantic islands.

596 *Hydrobiologia* **440**, 3-17.

597 Heape, W. (1888) Preliminary report upon the fauna and flora of Plymouth Sound. *Journal of*

598 *the Marine Biological Association of the United Kingdom* **1**, 153-193.

599 Hess, J.E., Campbell, N.R., Close, D.A., Docker, M.F., Narum, S.R. (2013) Population

600 genomics of Pacific lamprey: adaptive variation in a highly dispersive species.

601 *Molecular Ecology* **22**, 2898-2916.

602 Humphries, N.E., Queiroz, N., Dyer, J.R., *et al.* (2010) Environmental context explains Lévy

603 and Brownian movement patterns of marine predators. *Nature* **465**, 1066-1069.

604 Hunter, E., Metcalfe, J.D., Arnold, G.P., & Reynolds, J.D. (2004). Impacts of migratory

605 behaviour on population structure in North Sea plaice. *Journal of Animal Ecology*, **73**,

606 377-385.

607 Iglésias, S.P., Toulhoat, L. and Sellos, D. Y. (2010), Taxonomic confusion and market

608 mislabelling of threatened skates: important consequences for their conservation status.

609 *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**, 319–333.

610 Ingólfsson, A. (1995) Floating clumps of seaweed around Iceland: natural microcosms and a

611 means of dispersal for shore fauna. *Marine Biology*, **122**, 13-21.

612 Johnson, M.P., Burrows, M.T., Hartnoll, R.G., Hawkins, S.J. (1997) Spatial structure on

613 moderately exposed rocky shores: patch scales and the interactions between limpets and

614 algae. *Marine Ecology Progress Series* **160**, 209-215.

615 Johnson, M.P., Burrows, M.T., Hawkins, S.J. (1998) Individual based simulations of the

616 direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Marine Ecology*

617 *Progress Series* **169**, 179-188.

618 Jolly, M., Maitland, P., Genner, M. (2011) Genetic monitoring of two decades of

619 hybridization between allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*).

620 *Conservation Genetics* **12**, 1087-1100.

- Jolly, M.T., Aprahamian, M.W., Hawkins, S.J., Henderson, P.A., Hillman, R., O'Maoiléidigh, N., Maitland, P.S., Piper, R. & Genner, M.J. (2012) Population genetic structure of protected allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*). *Marine Biology* **159**, 675-687.
- Jorgensen, S.J., Reeb C.A., Chapple T.K., Anderson S., Perle C., Van Sommeran S.R., Fritz-Cope, C., Brown A.C., Klimley A.P., Block B.A. (2010). Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B* **277**, 679–688
- Kendall, M., Bowman, R., Williamson, P., Lewis, J. (1982) Settlement patterns, density and stability in the barnacle *Balanus balanoides*. *Netherlands Journal of Sea Research* **16**, 119-126.
- Kleiber, P., Argue, A.W., Kearney, R.E. (1987) Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1122-1134.
- Kohler, N.E., Turner, P.A. (2001) Shark tagging: a review of conventional methods and studies. In: *The behavior and sensory biology of elasmobranch fishes: an anthology in memory of Donald Richard Nelson*. Springer, pp. 191-224.
- Koufopanou, V., Reid, D.G., Ridgway, S.A., Thomas, R.H. (1999) A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular phylogenetics and evolution* **11**, 138-156.
- Lester, R. (1990) Reappraisal of the use of parasites for fish stock identification. *Marine and Freshwater Research* **41**, 855-864.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237-240.
- Lewis, J.R., Bowman, R.S. (1975) Local habitat induced variations in population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology* **17**, 165-203. [In English].
- Lima, F.P., Queiroz, N., Ribeiro, P.A., Hawkins, S.J., Santos, A.M. (2006) Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography* **33**, 812-822.
- Lima, F.P., Ribeiro, P.A., Queiroz, N., *et al.* (2007) Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Global Change Biology* **13**, 2065-2077.

655 Lowe, W.H., Allendorf, F.W. (2010) What can genetics tell us about population
656 connectivity? *Molecular Ecology* **19**, 3038-3051.

657 MacArthur, R.H., Wilson, E.O. (1967) The theory of island biogeography: monographs in
658 population biology. *Princeton University*.

659 Martins, G.M., Jenkins, S.R., Hawkins, S.J., Neto, A.I., Medeiros, A.R., Thompson, R.C.
660 (2011) Illegal harvesting affects the success of fishing closure areas. *Journal of the*
661 *Marine Biological Association of the United Kingdom* **91**, 929-937.

662 Martins, G.M., Jenkins, S.R., Hawkins, S.J., Neto, A.I., Thompson, R.C. (2008) Exploitation
663 of rocky intertidal grazers: population status and potential impacts on community
664 structure and functioning. *Aquatic Biology* **3**, 1-10.

665 McMichael, G.A., Eppard, M.B., Carlson, T.J., Carter, J.A., Ebberts, B.D., et al. (2010) The
666 juvenile salmon acoustic telemetry system: a new tool. *Fisheries* **35**, 9-22.

667 Meng, H.J., Stocker, M. (1984) An evaluation of morphometrics and meristics for stock
668 separation of Pacific herring (*Clupea harengus pallasii*). *Canadian Journal of Fisheries*
669 *and Aquatic Sciences* **41**, 414-422.

670 Metcalfe, J.D., Arnold, G.P., McDowall, P.W. (2002) Migration. In: *Handbook of fish*
671 *biology and fisheries*. Vol. 1. (Eds. P.J.B. Hart, J.D. Reynolds), Blackwell Scientific,
672 Oxford, pp. 175–199.

673 Mieszkowska, N., Sugden, H., Firth, L., Hawkins, S. (2014) The role of sustained
674 observations in tracking impacts of environmental change on marine biodiversity and
675 ecosystems. *Philosophical Transactions of the Royal Society A: Mathematical, Physical*
676 *and Engineering Sciences* **372**, 20130339.

677 Mork, J., Ryman, N., Ståhl, G., Utter, F., Sundnes, G. (1985) Genetic variation in Atlantic
678 cod (*Gadus morhua*) throughout its range. *Canadian Journal of Fisheries and Aquatic*
679 *Sciences* **42**, 1580-1587.

680 Nathan, R., Perry, G., Cronin, J.T., Strand, A.E., Cain, M.L. (2003) Methods for estimating
681 long-distance dispersal. *Oikos* **103**, 261-273.

682 Navarro, P., Ramírez, R., Tuya, F., Fernández-Gil, C., Sánchez-Jerez, P., Haroun, R. (2005)
683 Hierarchical analysis of spatial distribution patterns of Patellid limpets in the Canary
684 Islands. *Journal of Molluscan Studies* **71**, 67-73.

685 Neat, F., Pinto, C., Burrett, I., et al. (2014) Site fidelity, survival and conservation options for
686 the threatened flapper skate (*Dipturus cf. intermedia*). *Aquatic Conservation: Marine*
687 *and Freshwater Ecosystems* **2**, 6-20.

688 Nichols, O., Tschertter, U. (2011) Feeding of sea lampreys *Petromyzon marinus* on minke
689 whales *Balaenoptera acutorostrata* in the St Lawrence Estuary, Canada. *Journal of*
690 *Fish Biology* **78**, 338-343.

691 Nielsen, E.E., Hemmer-Hansen, J., Larsen, P.F., Bekkevold, D. (2009) Population genomics
692 of marine fishes: identifying adaptive variation in space and time. *Molecular Ecology*
693 **18**, 3128-3150.

694 Nobre, A. (1940) *Fauna malacológica de Portugal I. Moluscos marinhos e das águas*
695 *salobras*. Porto. 807pp.

696 Nunez, M.A., Relva, M.A., Simberloff, D. (2008) Enemy release or invasional meltdown?
697 Deer preference for exotic and native trees on Isla Victoria, Argentina. *Austral Ecology*
698 **33**, 317-323.

699 Pawsons, M., Vince, M. (1999) Management of shark fisheries in the northeast Atlantic . In:
700 *Case Studies of the Management of Elasmobranch Fisheries. FAO Fisheries Technical*
701 *Paper 378/1*. (Ed. R. Shotton), Food and Agriculture Organization of the United
702 Nations, Rome, pp. 1-46.

703 Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., Walters, C.J. (1998) Patterns of
704 covariation in survival rates of British Columbian and Alaskan sockeye salmon
705 (*Oncorhynchus nerka*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **55**,
706 2503-2517.

707 Peterson, D. A., Hilborn, R., & Hauser, L. (2014). Local adaptation limits lifetime
708 reproductive success of dispersers in a wild salmon metapopulation. *Nature*
709 *Communications*, 5. 3696.

710 Pita, A., Perez, M., Cervino, S., Presa, P. (2011) What can gene flow and recruitment
711 dynamics tell us about connectivity between European hake stocks in the Eastern North
712 Atlantic? *Continental Shelf Research* **31**, 376-387.

713 Priede, I. (1984) A basking shark (*Cetorhinus maximus*) tracked by satellite together with
714 simultaneous remote sensing. *Fisheries Research* **2**, 201-216.

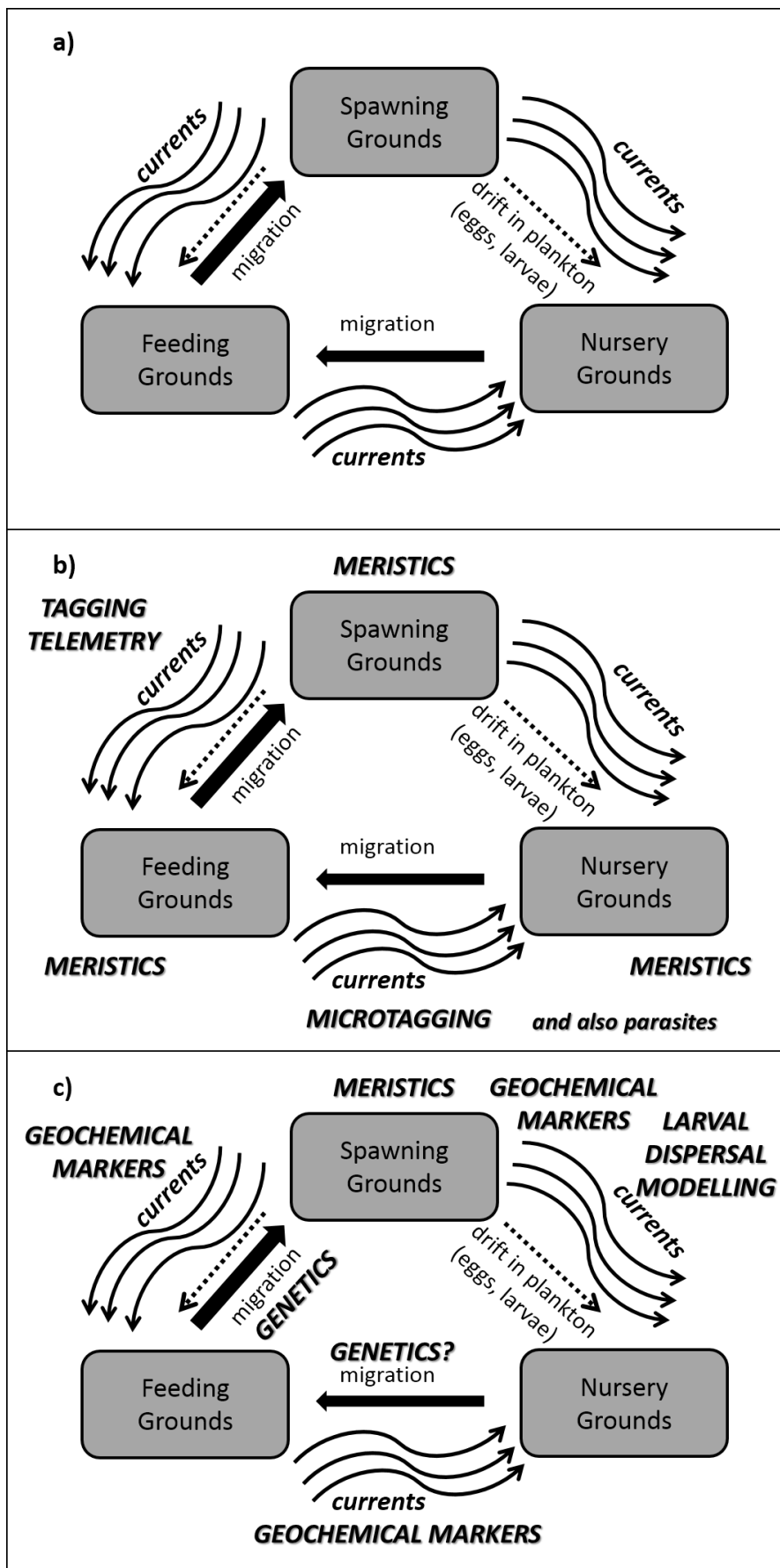
715 Quinn, T.P., Rich Jr, H.B., Gosse, D., & Schtickzelle, N. (2012). Population dynamics and
716 asynchrony at fine spatial scales: a case history of sockeye salmon (*Oncorhynchus*
717 *nerka*) population structure in Alaska, USA. *Canadian Journal of Fisheries and*
718 *Aquatic Sciences*, **69**, 297-306.

719 Ribeiro, P.A., Branco, M., Hawkins, S.J., Santos, A.M. (2010) Recent changes in the
720 distribution of a marine gastropod, *Patella rustica*, across the Iberian Atlantic coast did

- not result in diminished genetic diversity or increased connectivity. *Journal of Biogeography* **37**, 1782-1796.
- Righton, D., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H. et al. (2010). Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Marine Ecology Progress Series* 420, 1-13
- Righton, D., Kjesbu, O., Metcalfe, J. (2006) A field and experimental evaluation of the effect of data storage tags on the growth of cod. *Journal of Fish Biology* **68**, 385-400.
- Russell, E.S. (1931) Some theoretical considerations on the “overfishing” problem. *Journal du Conseil* **6**, 3-20.
- Sa-Pinto, A., Branco, M., Sayanda, D., Alexandrino, P. (2008) Patterns of colonization, evolution and gene flow in species of the genus *Patella* in the Macaronesian Islands. *Molecular Ecology* **17**, 519-532.
- Schtickzelle, N., Quinn, T.P. (2007) A metapopulation perspective for salmon and other anadromous fish. *Fish and Fisheries* **8**, 297-314.
- Schunter, C., Carreras-Carbonell, J., Macpherson, E., et al. (2011) Matching genetics with oceanography: directional gene flow in a Mediterranean fish species. *Molecular Ecology* **20**, 5167-5181.
- Shepherd, J. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil* **40**, 67-75.
- Siegfried, W., Hockey, P., Branch, G. (1994) The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa—an overview. In: *Rocky Shores: Exploitation in Chile and South Africa*. Springer, pp. 1-15.
- Simpson, S.D., Harrison, H.B., Claereboudt, M.R., & Planes, S. (2014). Long-distance dispersal via ocean currents connects Omani clownfish populations throughout entire species range. PLoS ONE, 9, e107610.
- Sims, D., Southall, E., Metcalfe, J., Pawson, M. (2005) Basking shark population assessment. Final project report. Global Wildlife Division, Department for Environment. *Food and Rural Affairs, London* **87**.
- Sims, D.W. (2008) Sieving a living: A review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. *Advances in Marine Biology* **54**, 171-220.
- Sims, D.W. (2010) Tracking and analysis techniques for understanding free-ranging shark movements and behaviour. In *Biology of Sharks and their Relatives, Vol. II*

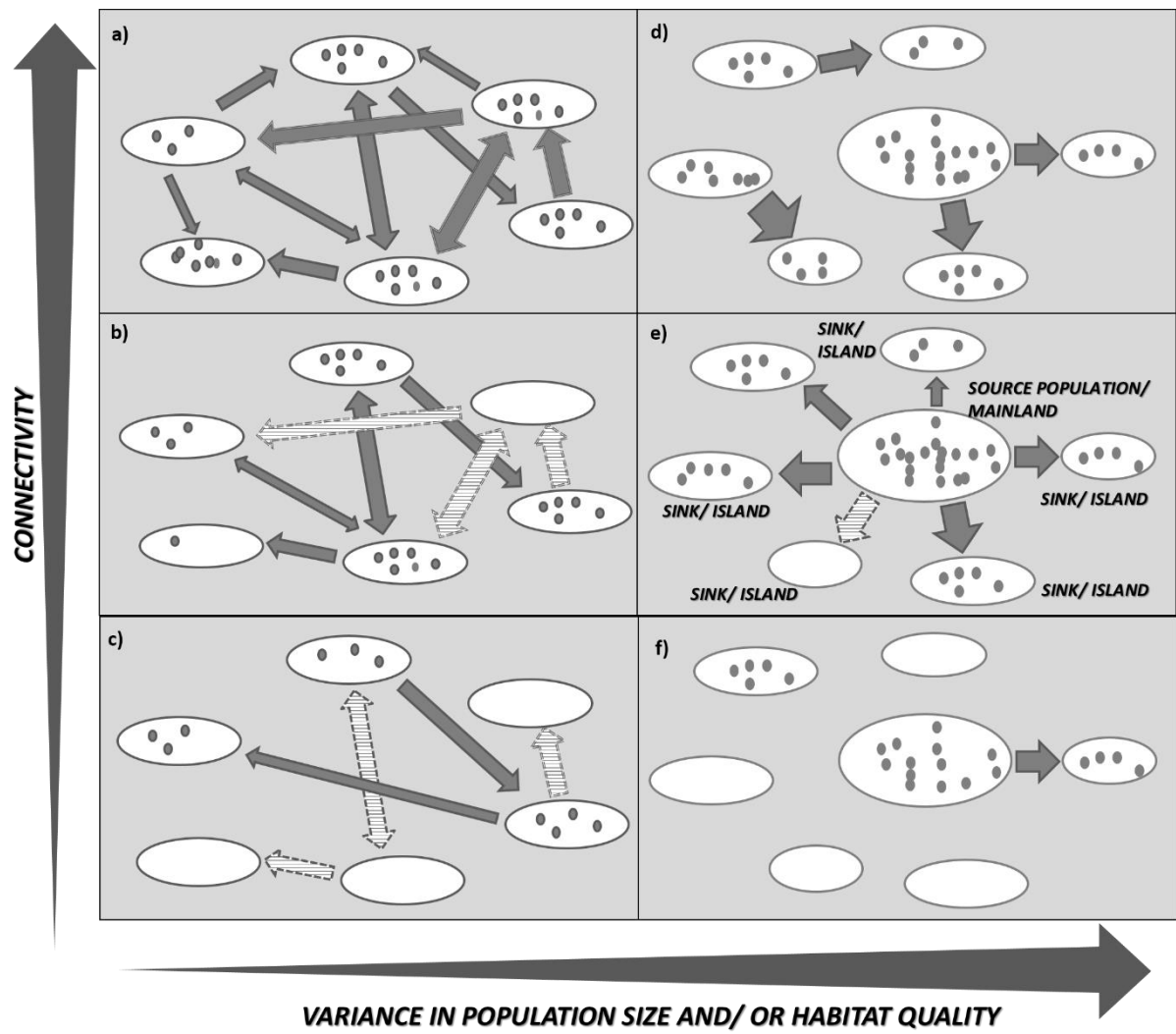
- Biodiversity, Adaptive Physiology, and Conservation* (eds, J. Carrier, M. Heithaus, J. Musick), p.351-392. Boca Raton, USA: CRC Press.
- Sims, D.W., Queiroz, N., Humphries, N.E., Lima, F.P., Hays, G.C. (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. *Plos One* **4**, e7351.
- Sims, D.W., Reid, P.C. (2002) Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland. *Fisheries Oceanography* **11**, 59-63.
- Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C., Metcalfe, J.D. (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series* **248**, 187-196.
- Skalski, J.R., Smith, S.G., Iwamoto, R.N., Williams, J.G., Hoffmann, A. (1998) Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1484-1493.
- Slatkin, M. (1993) Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**, 264-279.
- Smedbol, R.K., & Wroblewski, J.S. (2002). Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fisheries Research*, **55**, 161-174.
- Smith, P.J., & Jamieson, A. (1986). Stock discreteness in herrings: a conceptual revolution. *Fisheries Research*, **4**, 223-234.
- Sousa, L.L., Seabra, R., Wethey, D.S., *et al.* (2012) Fate of a climate-driven colonisation: Demography of newly established populations of the limpet *Patella rustica* Linnaeus, 1758, in northern Portugal. *Journal of Experimental Marine Biology and Ecology* **438**, 68-75.
- Southall, E.J., Sims, D.W., Witt, M.J., Metcalfe, J.D. (2006) Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the North-east Atlantic. *Biological Conservation* **132**, 33-39.
- Stewart, I.J., Hilborn, R., Quinn, T.P. (2003) Coherence of observed adult sockeye salmon abundance within and among spawning habitats in the Kvichak River watershed. *Alaska Fishery Research Bulletin* **10**, 28-41.
- Tanner, S.E., Perez, M., Presa, P., Thorrold, S.R., Cabral, H.N. (2014) Integrating microsatellite DNA markers and otolith geochemistry to assess population structure of

- European hake (*Merluccius merluccius*). *Estuarine, Coastal and Shelf Science* **142**, 68-75.
- Templado, J. (1997) La lapa ferruginea. *Biologica* **6**, 80–81.
- Thorrold, S.R., Jones, G.P., Hellberg, M.E., *et al.* (2002) Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science* **70**, 291-308.
- Turner, K., Righton, D., Metcalfe, J. (2002) The dispersal patterns and behaviour of North Sea cod (*Gadus morhua*) studied using electronic data storage tags. In: *Aquatic Telemetry*. Springer, pp. 201-208.
- Waples, R.S. (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity* **89**, 438-450.
- Wearmouth, V.J., McHugh, M.J., Humphries, N.E., Naegelen, A., Ahmed, M.Z., Southall, E.J., Reynolds, A.M., Sims, D.W. (2014) Scaling laws of ambush predator ‘waiting’ behaviour are tuned to a common ecology. *Proceedings of the Royal Society B* **281**, 20132997.
- Weber, L.I., Hawkins, S.J. (2002) Evolution of the limpet *Patella candei* d’Orbigny (Mollusca, Patellidae) in Atlantic archipelagos: human intervention and natural processes. *Biological Journal of the Linnean Society* **77**, 341-353.
- Weber, L.I., Hawkins, S.J. (2005) *Patella aspera* and *P. ulyssiponensis*: genetic evidence of speciation in the North-east Atlantic. *Marine Biology* **147**, 153-162.
- Wilkie, M.P., Turnbull, S., Bird, J., Wang, Y.S., Claude, J.F., Youson, J.H. (2004) Lamprey parasitism of sharks and teleosts: high capacity urea excretion in an extant vertebrate relic. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **138**, 485-492.
- Wit, P., Palumbi, S.R. (2013) Transcriptome-wide polymorphisms of red abalone (*Haliotis rufescens*) reveal patterns of gene flow and local adaptation. *Molecular Ecology* **22**, 2884-2897.



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817 Fig. 1



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819 Fig. 2

